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Cuticular characters adapted to volcanic stress in a new Cretaceous cycad leaf from Patagonia, Argentina. Considerations on the stratigraphy and depositional history of the Baqueró Formation

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Abstract

The cuticle of a new cycad, *Pseudoctenis ornata* Archangelsky et al., *sp. nov.* is described and discussed in relation to the physical paleoenvironment in which the plant lived. The specimens occur in the Early Cretaceous Baqueró Formation, near Estancia El Verano in the Santa Cruz Province, Argentina. A detailed stratigraphic section records four facies, namely (1) fluvial channel, (2) flood plain, (3) lacustrine, and (4) flat and extended plains. A detail of each facies is provided. *Pseudoctenis* cuticles are found in the flood plain facies; the other components of the plant association are *Gleichenites*, *Araucaria* and *Taeniopteris*. The depositional history of this succession is related to a braided river that periodically received volcanic ash. Plants grew until complete burial by ash. Leaves of *Pseudoctenis* are pinnate, hypostomatic, with polycyclic stomata that form ill-defined rows. Abundant papillae and hair bases are present, especially on the lower cuticle. Comparisons are made with other *Pseudoctenis* species found in the same formation, and in other regions of the world. It is suggested that the paleoenvironment had a strong influence on the vegetation, especially the ash fall, and that it may have played a role in the formation of xeromorphic structures that characterize several gymnosperms present in this stratigraphic unit, including *Pseudoctenis ornata*. The lack of burning features on the cuticle suggests a cold ash fall. This fall probably was responsible for changes in edaphic patterns and atmospheric conditions that governed the growth and distribution of plant communities during the deposition of the Baqueró Formation.

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1. Introduction

Cuticular analysis has been a useful tool in taxonomic studies of the Cretaceous Ticó flora from the Santa Cruz province, Argentina (Archangelsky, 1963; Menéndez, 1966; Archangelsky and Taylor, 1986). Gymnosperms, represented by several orders (i.e. Coniferales, Bennettitales, Ginkgoales, Cycadales and putative pteridosperms), all have a well-developed cuticle. Because of the fine preservation, several of these cuticles have been studied at the ultrastructural level (Archangelsky et al., 1986; Archangelsky and Taylor, 1986). It has also been suggested that volcanic ash may have played a role in the fossilization process (Archangelsky and Taylor, 1986) because plants are found in strata related to volcaniclastic rocks (mainly tuffs).

Recent field studies of the fossil plant bearing unit (Baqueró Formation) revealed that sedimentation took place in a continental fluviatile environment during a time of intense volcanic activity that produced heavy ash fall (Cravero and Dominguez, 1993). We now intend to further inquire the significance that ash fall may have had on the development of cuticular structures considering that this membrane serves to protect basic leaf functions vital for plant subsistence.

This area has been surveyed since the 1920s, when Burton Clark collected the first plant fossils that Berry (1924) later described. Although several geologists and paleontologists made extensive collections in the area, there were no references to plant cuticles. The present record opens the possibility for further field research because cuticles were found thus far only in Ticó, Bajo Grande and Bajo Tigre localities (Fig. 1). The new site at Meseta Baqueró, near Estancia El Verano (Fig. 1) contains well preserved cuticles that show little (if any) post mortem transport. The type locality of the Baqueró Formation, Punta del Barco, is close to the sections described here.

Leaves of *Pseudoctenis* are among the most frequent fossils at this site. The next most common plant is the conifer *Araucaria grandifolia* Feruglio (Feruglio, 1951) (Fig. 2). Remains of *Taeniopteris* sp. (without cuticle) and *Gleichenites* spp. are also well represented at this site.

The cuticule of this cycad plant shows several xeromorphic characters that require an interpretation based not only on ecological anatomy, but also on the physical environments in which the plant lived. This last parameter is discussed here in detail, together with the description of the fossil in the hope that combined research will shed further light on the understanding of the vegetation history during the Early Cretaceous in Patagonia.

2. Materials and methods

The plants occur in the Upper Member of the Baqueró Formation (sensu Archangelsky, 1967; not Hechem and Homovc, 1988). This area is the type locality of the unit of which several sections have been studied (Feruglio, 1949; Stipanicic and Reig, 1957). New detailed sections showing stratigraphy and fossil occurrences are presented in Fig. 3. The age of the unit is probably Early Aptian (Romero and Archangelsky, 1986).

Fossils are embedded in tuffs, with no specific orientation. They are mainly represented by cutinized leaves that project from the matrix when the rock is split. Sediments are not laminated, suggesting that there was little or no transport of the leaf material (Fig. 2). Fossil branches with attached leaves may attain a length of c. 1 m. Tuffs are not compacted and easily disaggregate. As a result plant remains leave poor impressions on the surface; however, excellent cuticles are preserved.

Cuticles were prepared for study for both optical and electron microscopy. The material is easily separated from the matrix and only needs cleaning with dilute nitric acid followed by ammonium hydroxide. Specimens were mounted in glycerine-jelly for observation with light microscopy, or directly on cylindrical stubs and coated with gold-palladium for scanning electron microscopy. SEM observations were made with a JEOL JMS 100 instrument (at 15 kV) at the La Plata Natural History Museum using AGFAPAN APX 100 film. For transmission electron microscopy

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(TEM) cuticle frag
low viscosity resin
lined by Archangels
cut with a diamon

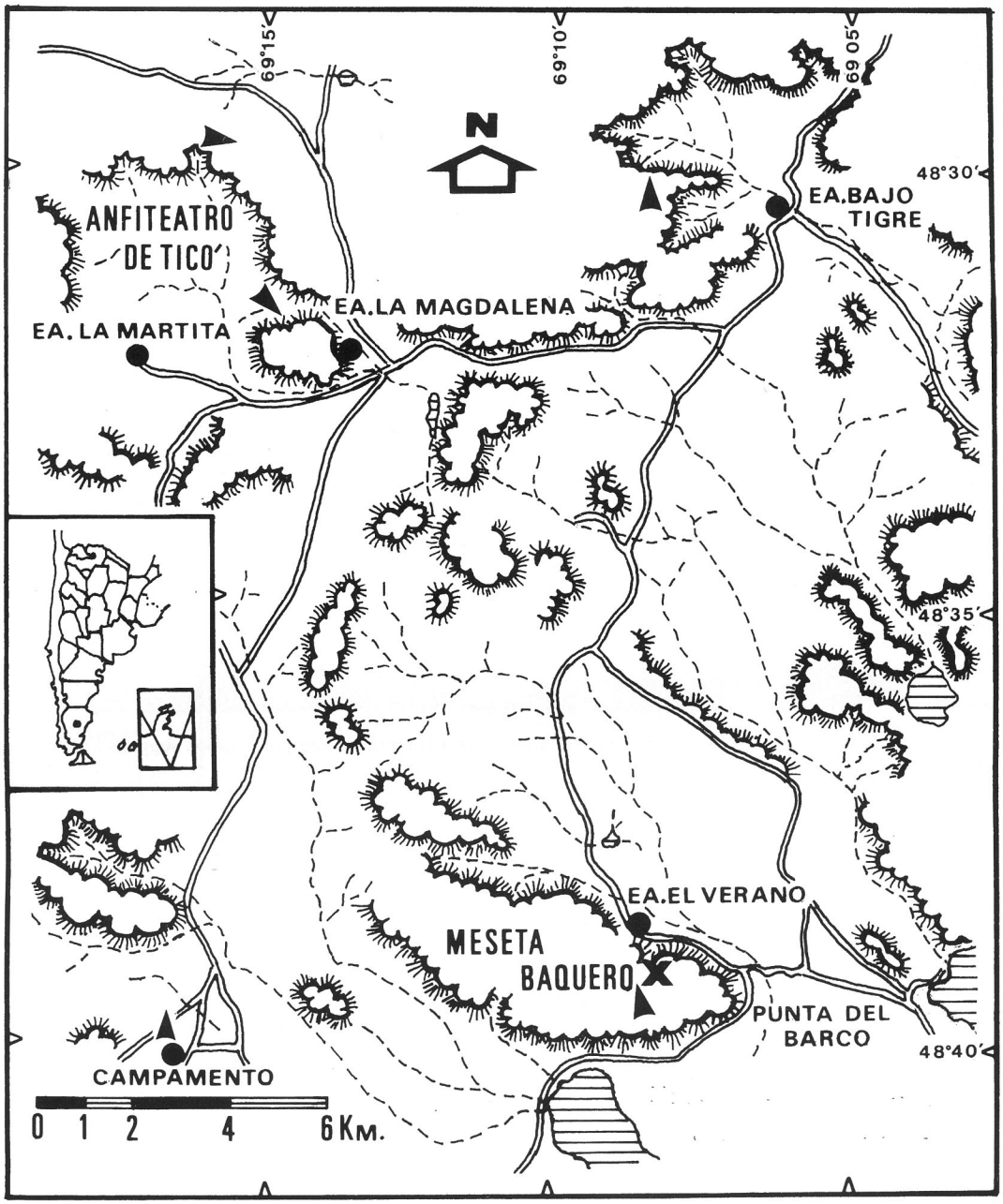

Fig. 1. Map showing the location of the studied area (x). Arrows indicate paleocurrents.

(TEM) cuticle fragments were embedded in Spurr low viscosity resin following the technique outlined by Archangelsky et al. (1986). Sections were cut with a diamond knife on a SORVAL manual ultramicrotome, and mounted in single hole grids coated with Formvar, and stained with $KMnO_4$ (5–10 min) and Uranil acetate (30 s). Observations were made on a JEOL JEM 100C at the

Fig. 2. *Araucaria grandifolia* Feruglio. Branches included in a tuff (pyropsammite). Their preservation suggests little or no transport and a rapid entombment in volcanic ash (photolens is 3.5 cm in diameter).

CEVAN-CONICET Institute. Kodak plates were used for photography. A Leitz Dialux microscope was used for optical observations and photomicrographs were taken with a Canon FN camera using Kodak TMX film.

The type specimens have been deposited at the Paleontological Museum "E. Feruglio" of Trelew, Chubut Province (MPEF Pb). Other specimens, slides, SEM stubs, TEM sections and negatives are stored in the Paleobotanical collection of the Buenos Aires Natural History Museum (BA Pb).

3. Stratigraphy

The section located near Estancia El Verano (Fig. 1) is 135 m thick. It comprises sediments of the Early Cretaceous Baqueró Formation (68 m) and the middle Tertiary Patagonia Formation (67 m). Both units lie sub-horizontally and are apparently conformable. The Baqueró Formation is composed of yellow, brown to gray epiclastic and pyroclastic rocks. They contain paleosols, several levels with silicified trunks or leaves, as well as traces of ant (BE = bioerosion) or worm (EN, EP = endichnia, epichnia bioturbations, respectively) activity.

Four facies can be recognized in the Baqueró Formation succession on the basis of stratification (geometry, thickness, contacts), composition and chromatic criteria: (1) fluvial channel, (2) flood plain, (3) lacustrine, and (4) flat and extended plains. The latter facies is rare at the type locality though abundant northwards, in the Bajo Tigre and southeastern Ticó Amphitheatre areas (Fig. 1). The channelized facies are better developed at the Ticó Amphitheatre NW section, where thick lenticular clast-supported conglomerates

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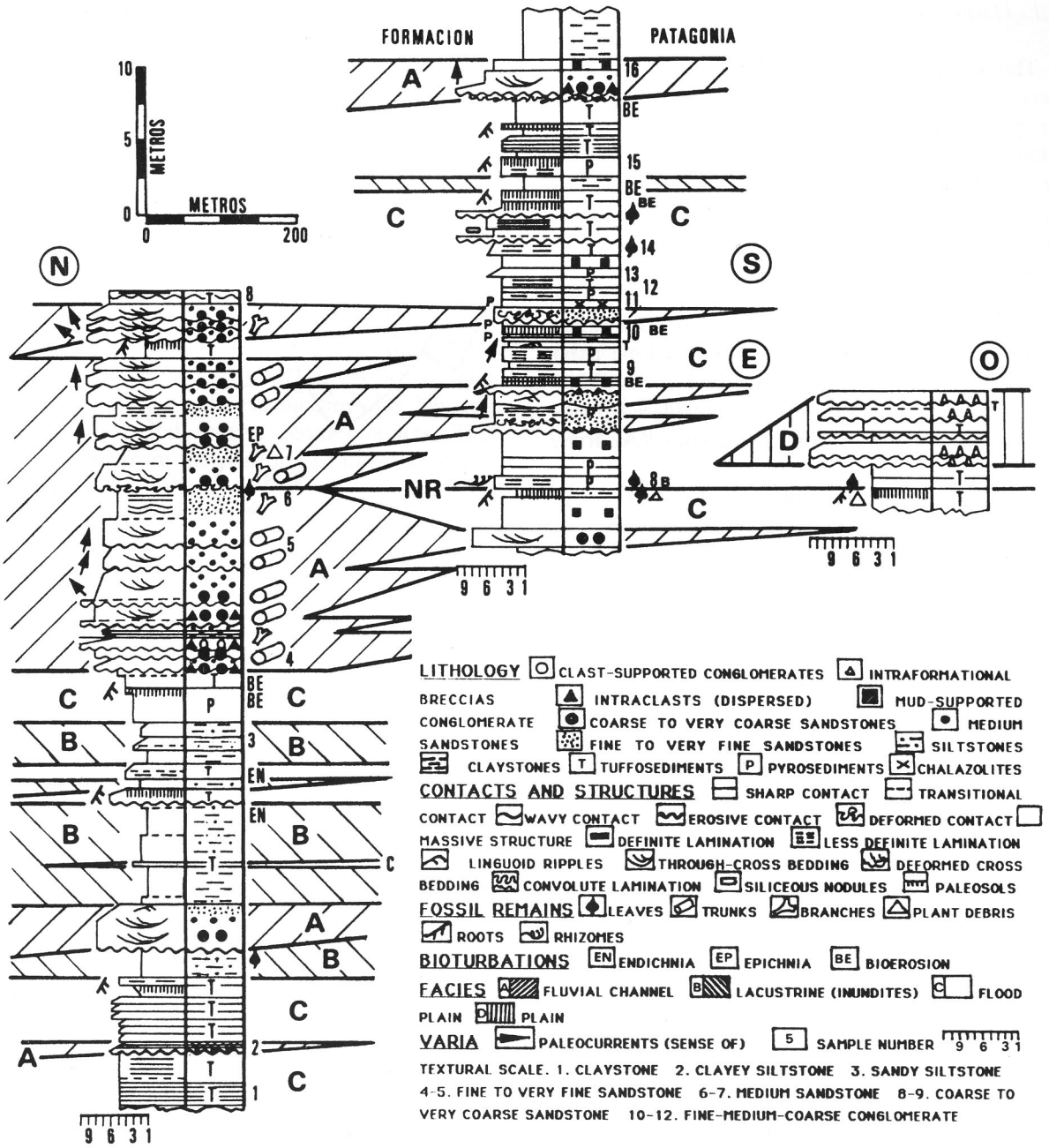


Fig. 3. Detailed stratigraphic section of the study area. N = north, S = south, E = east, O = west.

have been described by Caranza (1988). The lacustrine facies were recorded in the lower half of the Bajo Tigre Section where abundant and well preserved plant remains have been collected. The symbols used for fluviatile sediments are those of Miall (1982).

3.1. Fluvial channel facies

This facies is mainly integrated by medium to very coarse trough cross-bedded (*St*), laminated or thin tabular stratified (*Sh*) or massive (*Sm*) sandstones. Occasionally clast-supported conglomerates (*Gm*) and massive mudstones (*Fm*) are present. The *Gm* lithofacies contains imbricated and subrounded to rounded pebbles and cobbles of lithic composition (rhyolite and andesite lavas, together with rare ignimbrite fragments). The basal conglomerates also include flat to ovoidal tuffaceous intraclasts (with an up to 30 cm long axis) formed by erosion of the underlying rocks. They contain small roots and may be considered pedorelicts (Brewer, 1964) or edapholites (Andreis, 1981).

These rocks may be yellowish, brownish, reddish, blueish gray, and appear as shoestring bodies of lenticular shape in section; they occur in dm fining-upwards cycles and range up to 3 m thick. The most common cycles are the *Gm–St–Sh* and *Gm–St*, while *Sh–Sm–Fm* is rare. At least 19 cycles have been recognized in the main channel. The channels include abundant silicified trunks that range from splinters to logs 40 cm wide, and a few meters long. None contain roots. The largest logs were distributed at the base of the erosive channel while the smaller ones occurred mainly in cross-bedded structures. A few westward imbrications were recorded but most trunks are disposed parallel or subparallel to the prevailing currents (Fig. 4). On the basis of the cross-bedding structures and main channel orientations, we believe that the paleocurrents were usually directed northwards and occasionally to the west.

3.2. Flood plain facies

Flood plain facies are characterized by the exclusive participation of pyroclastic rocks, defined as pyro/tuffosediments owing to its primary (ash falls) or secondary (reworking by water) origin (see Teruggi et al., 1978; Mazzoni, 1986). The successions contain abundant yellow, light brown, gray or white laminated (sometimes including chalazolites), rare massive or rippled pyro/tuffo-psammites and scarce tuffo-conglomerates. Massive matrix-supported breccias, containing tuff clasts of volcanic origin were also found. Tabular or lenticular stratification types of centimeter or tens of centimeter thickness, and extending 100 m or more, are very common. Tuffs and breccias may show pedogenetic features, represented by poorly developed prismatic structures and axial roots, up to 15 cm long, with or without branching (Fig. 3). Above one paleosol rain prints and well preserved leaves were found (*Gleichenites*, pteridosperms), while the overlying pyropsammite contains *Pseudoctenis*, *Gleichenites*, *Araucaria* (Fig. 2), *Macrotaeniopteris* with cuticles, and in-situ rhizomes. Bioerosion structures (BE) produced by ant or worm activity occur in several layers.

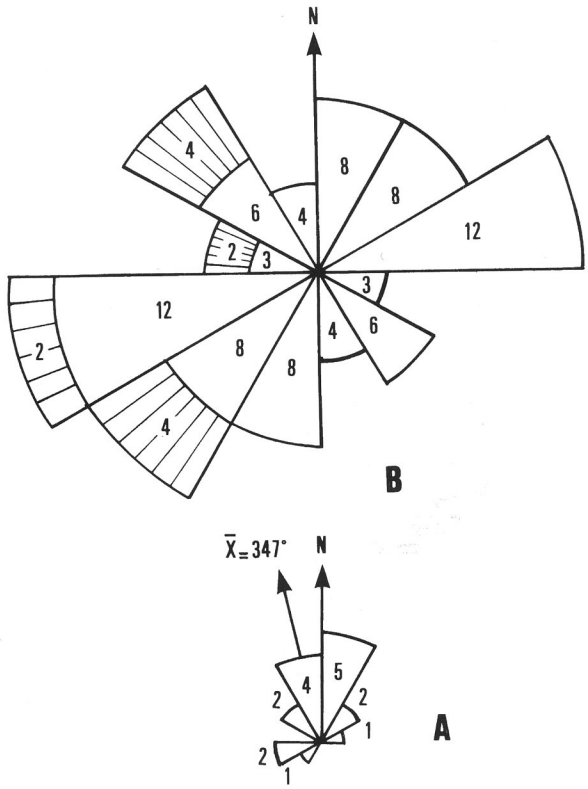


Fig. 4. Paleocurrents and distribution of trunks. (A) Orientation of crossed structures (with number of measurements). (B) Dispositon of trunks (with number of measurements). |||| = imbricated trunks.

3.3. Lacustrine facies

These facies are in the 2 m thickness range and are massive or laminated, composed of mudstones and siltstones of kaolinitic nature. They are olive gray, olive brown, dark brown or dark gray, and include several endichnia-type bioturbation horizons.

3.4. Flattened extended plains

These deposits are composed of gray, fine massive or faintly laminated tuffo- and pyro-psammites (?) and yellow intraformational breccias. The coarser deposits show shoestring geometry, lenticular in section, and erosive basal contacts. The clasts derived from the erosion of tuffo-psammites are angular or subangular, and measure up to 10 cm in diameter. Both tuffo-psephytes (breccias), and tuffo-psammites constitute up to 2 m thick fining-upward cycles.

4. Interpretation and depositional history

The succession at the site shows abundant occurrences of the channel, flood-plain and lacustrine facies, and localized flattened extended plain facies; facies have a definite vertical distribution (Fig. 3).

The lower half of the succession includes abundant lacustrine facies often associated with channel and flood-plain facies. They represent the persistent flooding of extended paleovalleys interrupted by short fluvial channel episodes, and are presumably related to the final filling of an older paleorelief by a fluvial system that was well-developed in the Campamento area (Fig. 1). The kaolinitic nature of the fine sediments is related to the erosion of kaolinic volcanic/ignimbritic rocks of the Chon-Aike Formation. The dominant lacustrine sequence was covered by flat and extended plain facies, e.g. in the Bajo Tigre area. They are similar to the facies described by Caranza (1988) at the Ticó Amphitheatre. The coarser facies may have also been deposited in small and shallow ephemeral rivers that cut and eroded extended plains formed by tuffo- and pyro-sediments. These finer facies were probably deposited under eolian activity. Consequently, the massive facies may represent paleoloess (tephric loess; Campbell, 1986), while the laminated varieties correspond to brief water reworking episodes (paleolehm?).

Channel facies are concentrated in the upper half of the sequence and include a 25 m thick body intertongued with, or covered by, flood plain facies. This association probably was deposited in wide and shallow valleys excavated in flat and extended plain facies and the underlying lacustrine facies.

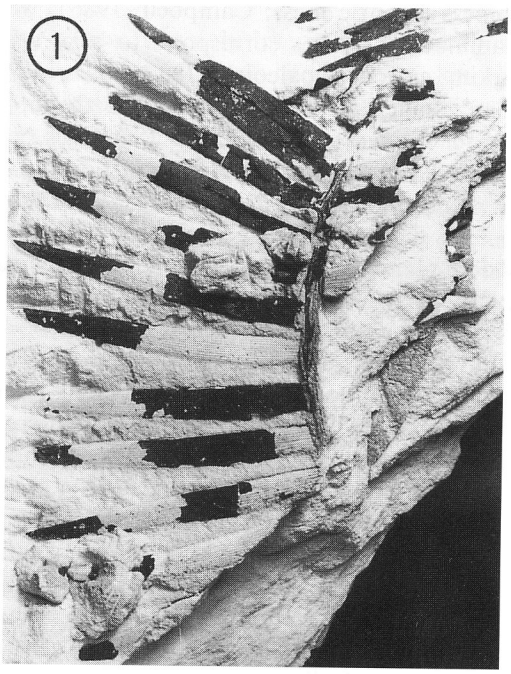
The concave-upward, lenticular channel bodies may have been produced by poorly hierarchisized, relatively low-sinuosity streams, and poor lateral channel mobility. The abundance of trough cross-bedding reflects the migration of 3-D, commonly linguoid, sandwaves in a distal braided river system (cf. Collinson, 1986). They show internal evidences of water stage fluctuations represented by reactivation surfaces, and a vertical decrease in set thickness. The abrupt waning of flow strength is represented by *Sh* and *Fm* facies (the "abandonment facies" of Collinson, 1986). Waters flowed northwards following the local paleoslope.

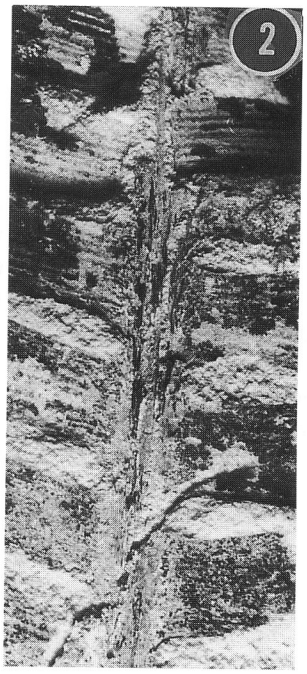
The abundance of small rootless logs suggests high-energy transport conditions. It is probable that the source area for the trees was at some distance from the Meseta Baqueró.

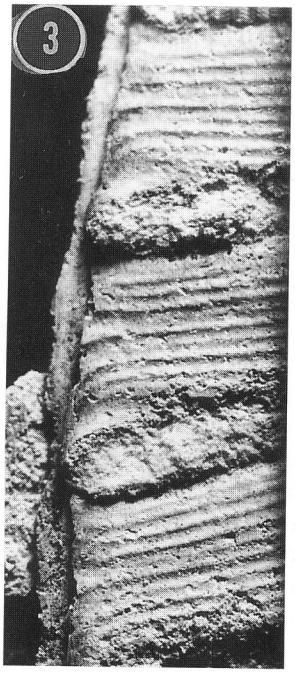
The braided river was probably confluent to the main river that flowed ESE, and was characterized by abundant conglomeratic facies as described by Caranza (1988) at the northwest corner of the Ticó Amphitheatre.

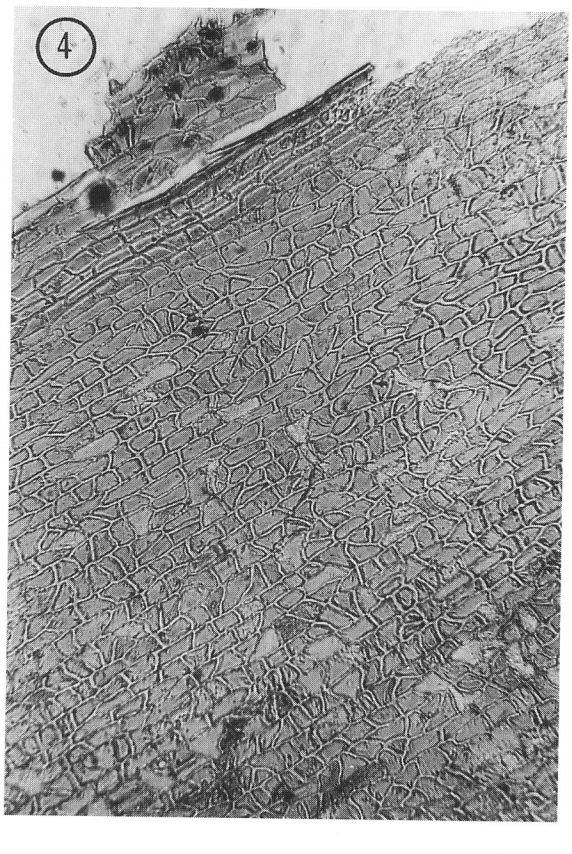
In the flood plain facies the presence of incipient paleosols in many pyrosediments (and also in the matrix-supported breccias) suggests that the ash fall was not continuous, thus providing time for soils to develop. The ash fall might have occurred simultaneously with plants growing. The laminations might be related to ash falling into small ponds or shallow lakes. Scarce ripples that show the same northward orientation as the river currents may suggest that the ponds/lakes were related to short flooding events that occurred in the valley. Long-term flooding episodes that are represented by an alternation of pyro- and tuffo-sediments suggest the erosion of former weakly lithified ash fall deposits.

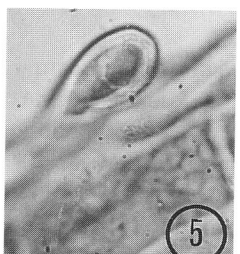
PLATE I

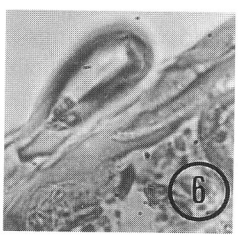


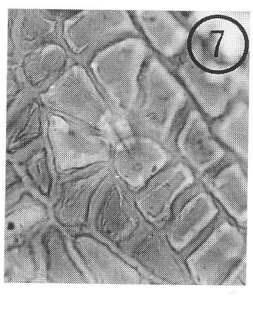


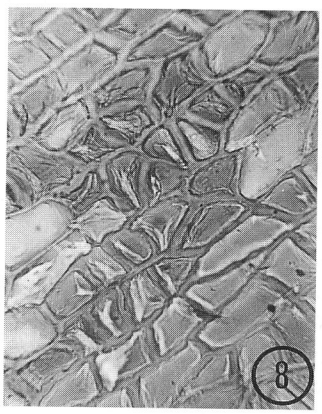


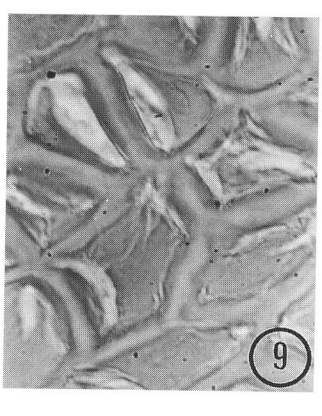












Periodically the flood-plain facies were covered by matrix-supported breccias. The presence of tuffs and volcanic fragments suggests that these rocks were generated by debris flows coming from regions of high relief, probably related to the erosion of flat and extended plains that bounded the valleys.

5. Taxonomy

Order CYCADALES

Pseudoctenis Seward, 1911, emend. Harris, 1964

Pseudoctenis ornata Archangelsky et al., *sp. nov.*

Holotype: MPEF Pb 6 (Plate I, 1).
Paratype: MPEF Pb 7 (Plate I, 2).
Other specimens studied: BA Pb 1217–1222. Slides, BA Pb p.m. 86, 87, 88.
Repository: Museo Paleontológico Egidio Feruglio, Trelew, Argentina, and Museo Argentino de Ciencias Naturales "B. Rivadavia", Buenos Aires, Argentina.
Type locality: Meseta Baqueró, Estancia El Verano, Santa Cruz Province, Argentina.
Stratigraphic horizon: Baqueró Formation, Early Cretaceous.
Etymology: The species name *ornata* refers to the ornament of the cuticle.

Diagnosis

Leaves pinnate with pinnae opposite to subopposite, laterally inserted at almost right angles, rachis longitudinally striated, pinnae linear to acuminate, tapering to an acute apex, expanded at base, up to 8 cm long and 0.8 cm wide, adjoining pinnae separated; veins up to 8 per pinna, straight to decurrent at base, parallel, single, reaching acute apex; leaves hypostomatic with upper cuticle thick, bearing occasional hollow papillae, short unicellular hairs and hair bases; epidermal cells rectangular, triangular, square-isodiametric, or occasionally oval, elongated at margins, lower cuticle showing veins and intervein areas as longitudinal bands, epidermal cells over veins forming rows, rows absent between veins, cells isodiametric to elongate; papillae hemispheric to elongate, one per cell, densely covering surface; stomata numerous and irregularly distributed or forming ill defined rows between veins, longitudinally to obliquely oriented, often with subsidiary cells in contact or shared; stomatal apparatus subcircular to oval with ring of papillae; stomata polycyclic with up to 4 cycles of subsidiary cells; guard cells sunken and thickened, elongate, differentiated into a polar and central area; upper cuticle consisting of outer lamellated layer and an inner granular zone; lower cuticle with outer homogeneous layer, externally lamellated, and inner layer that is lamellated and granular.

Description

The incomplete leaves are pinnate and estimated to have been up to 16 cm wide. The longest fragment measures 16 cm (holotype, Plate I, 1). Pinnae are opposite to subopposite, laterally inserted at almost right angles to a strong, longitudinally striated rachis which is up to 7 mm wide. Pinnae are linear to acuminate, up to 8 cm long and 0.8 cm wide, tapering to an acute apex and expanded at the base, both catadromically and

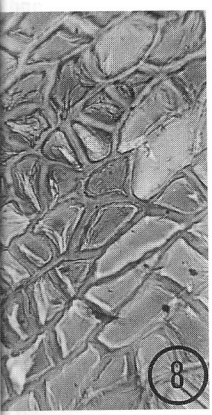
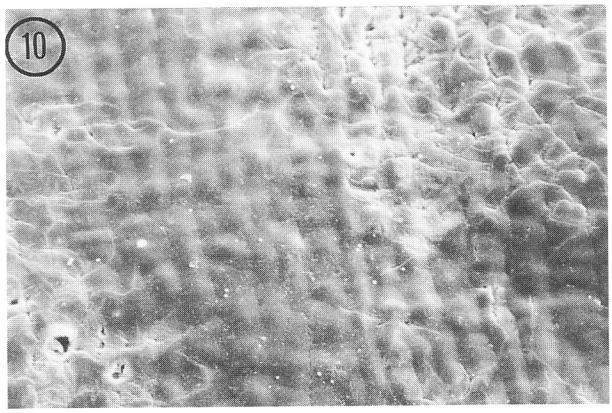
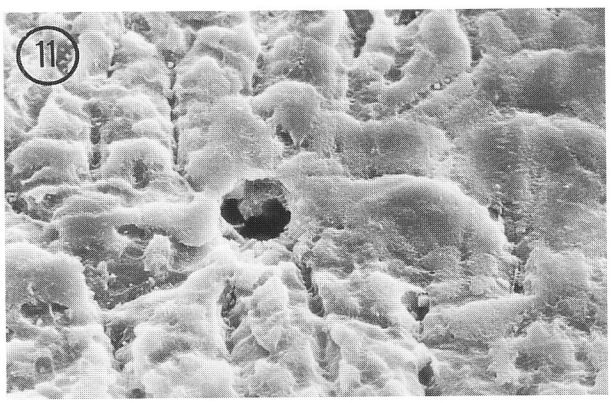


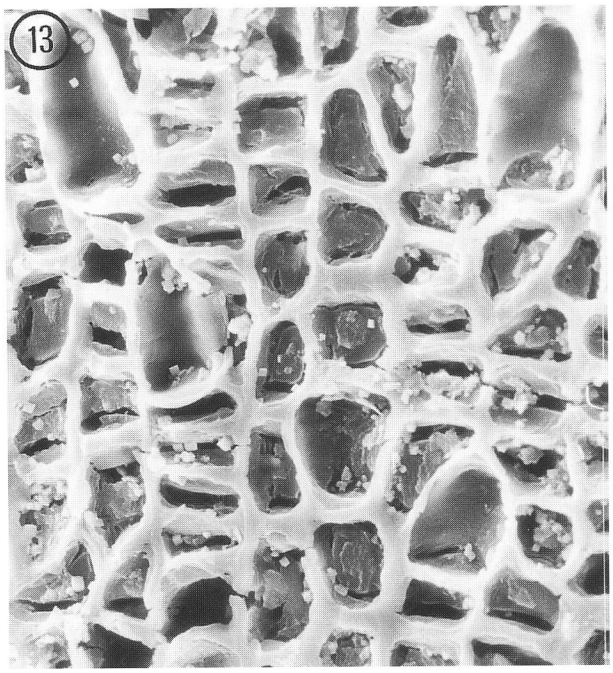
PLATE I

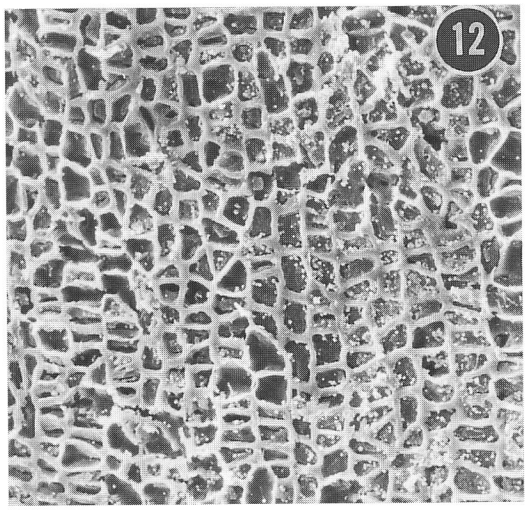
1. General features of the holotype (MPEF Pb 6). ×0.5.
2. A detail of the paratype (MPEF Pb 7) showing striated leaf rachis and pinnae insertion. ×2.
3. A detail showing the base of three pinnae expanded at base, and slightly decurrent venation. ×3.5.
4–9. Upper cuticle (slide BA Pb p.m. 87).
4. Distribution of epidermal cells. ×100.
5, 6. Different focal planes of a hollow, marginal papilla. ×600.
7. Hair base. ×200.
8. Group of thickened epidermal cells. ×200.
9. Detail of 8. ×600.

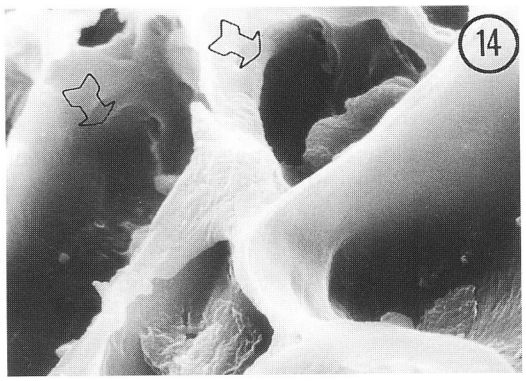
PLATE II

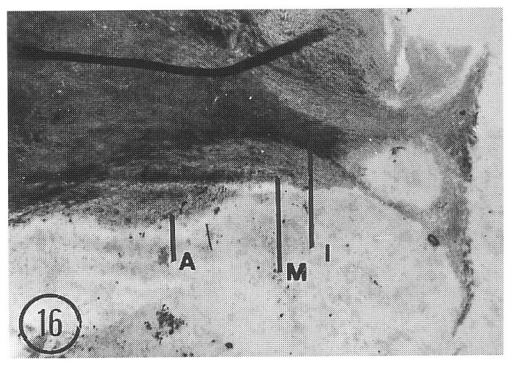












anadromically. Adjacent pinnae are separated up to 0.5 cm (usually 0.2–0.3 cm), i.e. less than their width (Plate I, 2, 3). There are up to 8 veins per pinna, each c. 0.6 mm thick, straight to slightly decurrent at their base. Vein concentration is 1.7 per mm or less (Plate I, 2, 3). Veins are parallel and single (only one bifurcation was observed), reaching the acute apex.

Two different cuticles have been observed. One lacks stomata (assumed to be the upper cuticle) while the other is characterized by abundant stomata (assumed to be the lower cuticle).

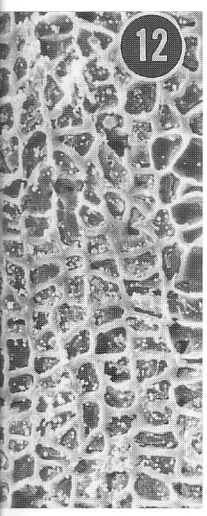
The upper cuticle is up to 8.5 μm thick (measured in folds), and occasionally bears hollow papillae (Plate I, 5, 6) and short unicellular hairs and broken hair bases (Plate I, 7) that are surrounded by radially oriented epidermal cells. Epidermal cells are rectangular, elongated at pinna margin, and up to 100 μm long; they are square-isodiametric, up to 60 μm on the rest of the lamina (Plate I, 4). Triangular–oval cells are also common. Epidermal cells often occur in rows, sometimes with an internal microgranular content. Periclinal walls are smooth, thickened, and usually thinest near anticlinal flanges (probably due to degradation). Groups of thickened cells (sclerotic nests) were also observed (Plate I, 8, 9).

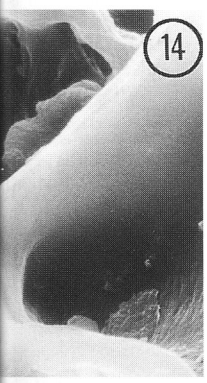
Epidermal cells are characterized by external longitudinal striae that cross at right angles by a less pronounced striations that define the contours of the epidermal cells (Plate II, 10). Areas with thickened cuticles surround a circular hole that corresponds to hair bases (Plate II, 10, 11). Epidermal cells that form files are best seen internally (Plate II, 12). Thinning of the cuticle along anticlinal flanges, as well as the pitting of the wall may be seen in this view (Plate II, 13, 14).

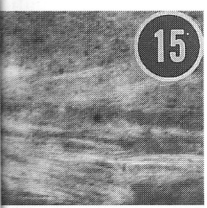
The periclinal wall consists of an external layer in which lamellation is present (Plate II, 15). Lamellae are compact and form bands up to 0, 3 μm thick; each is composed of 10 or more units. Individual lamellae are less than 10 nm thick. Anticlinal flanges show a solid internal layer (more electron dense) between a lighter granular layer and an outer, more porous, thin layer including compact dark granules (Plate II, 16). Anticlinal flanges may extend internally for 30 μm.

The lower cuticle is up to 6 μm thick and has clearly defined areas between veins that are arranged in longitudinal bands (Plate III, 17). Epidermal cells over veins are rectangular, elongated, and form ill defined rows, each cell up to 100 μm long and 30 μm wide with thickened periclinal walls. Cells between veins are isodiametric or elongate, and not arranged in rows; they are up to 75 μm long and 35 μm wide. Cells on margins elongated (Plate III, 17). Each cell is characterized by a hollow hemispheric to elongate papilla (Plate VI, 34, 35); papillae bases occasionally cover two cells. Papillae densely cover the surface, and each has strong internal striations (Plate III, 24). On the surface are continuous longitudinal ridges that form rows on veins that are less defined in stomatal bands between veins (Plate IV, 25). Papillae are present on ridges over all the surfaces except on margins where they are rarely present (Plate IV, 25). Circular holes that correspond to hair bases are located between ridges (Plate IV, 26).

Stomata are distributed irregularly or form ill defined rows between veins. They are rarely present over veins. Stomata are longitudinally to obliquely oriented (Plate III, 17; Plate IV, 27), and often have subsidiary cells in contact or they share a







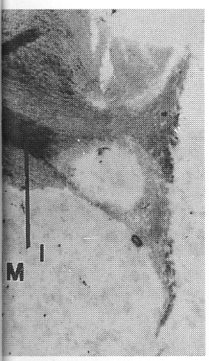
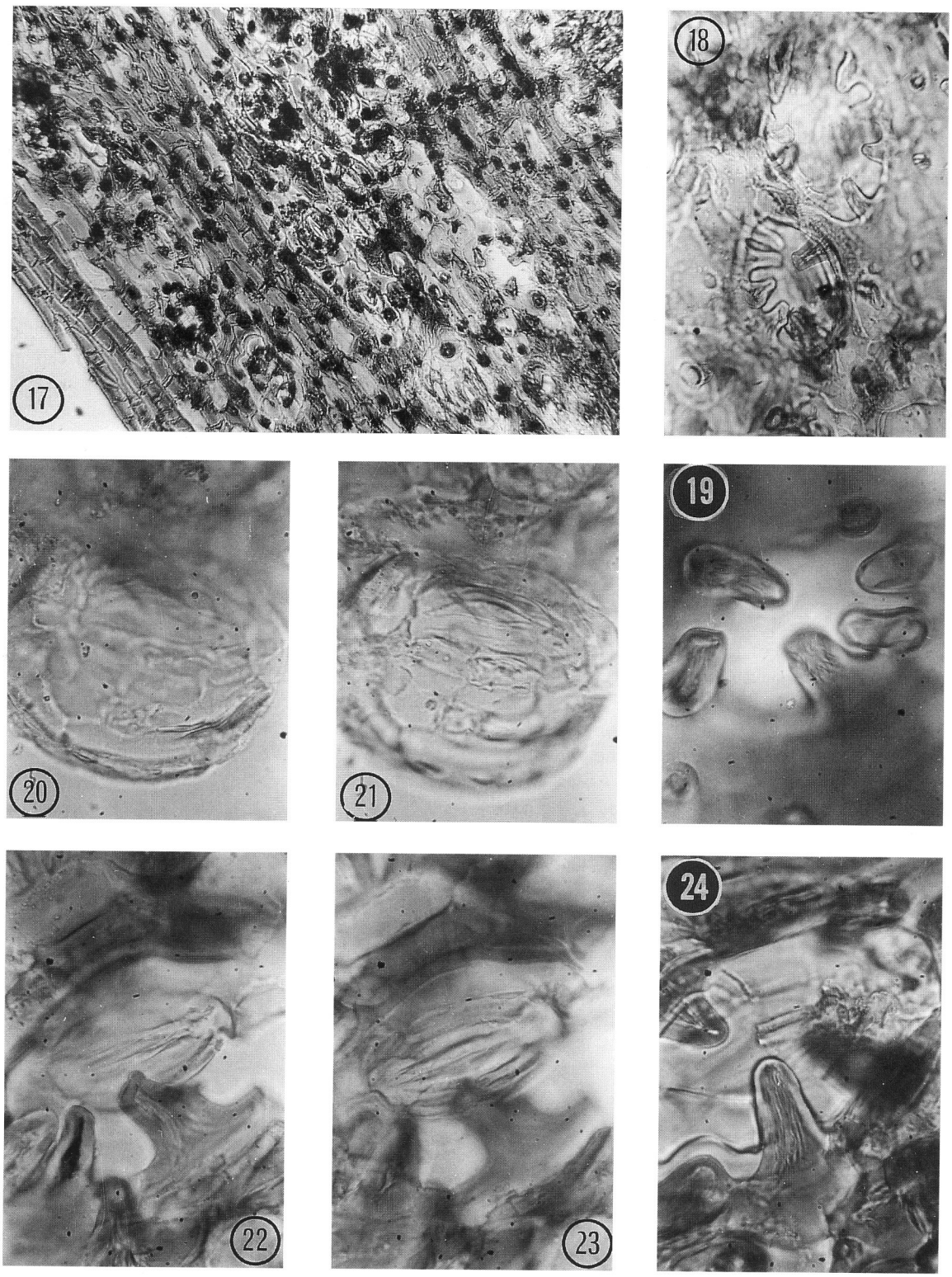


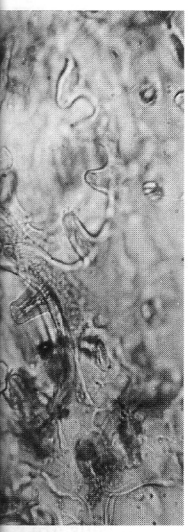
PLATE II

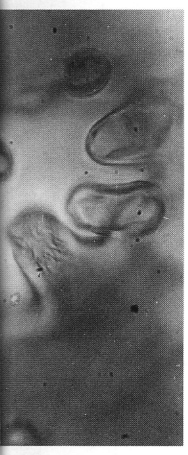
Upper cuticle.

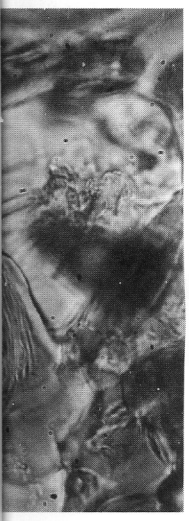
10. External longitudinal striae and hair bases. ×150.
11. Detail of a hair base. ×500.
12. Internal view of epidermal cells. ×150.
13. Anticlinal flanges and thin areas of periclinal cuticular membrane. ×500.
14. A detail to show pitting (arrows) of anticlinal flanges. ×1500.
15. Lamellation of cuticular membrane. ×50,000.
16. Cuticle layers in anticlinal flange. *I*=solid internal layer, *M*=lighter granular layer, *A*=basal layer including granules. ×3000.

PLATE III









common subsidiary cell (Plate III, 18; Plate IV, 25). The stomatal apparatus is subcircular to oval and up to 100 μm in diameter; a ring of papillae protect the orifice (Plate III, 18, 19; Plate IV, 25). Typically two lateral papillae are more developed than the other papillae that surround the mouth (Plate III, 19). Each stomatal complex consists of up to 4 cycles of 6 cells each that form a subsphaerical epistomatal chamber (Plate III, 20, 21; Plate IV, 29). Outer subsidiary cells are larger than inner subrectangular cells (Plate IV, 29). Guard cells are sunken and thickened. They are elongated and differentiated into a polar and central areas (Plate III, 22, 23). The stoma is strongly thickened on the outer and inner walls (Plate IV, 28). A central bridge-like structure occasionally develops between guard cells (Plate IV, 29). A strong continuous oval thickening that is more developed in both polar areas is seen over the external wall of guard cells (Plate IV, 28).

The lower cuticle is about 5 μm thick (Plate V, 33)and composed of an outer homogeneous layer (*A*) and a lower lamellated, granular layer (*B*). The outer layer is externally lamellated (*A*1) and internally homogeneus (*A*2), with irregular isodiametric areas showing lighter electron density. The *A*1 sublayer is approximately 0.04 μm thick, with individual lamellae that are about 3 nm. They are separated by translucent channels that anastomose, and are parallel to the surface (Plate V, 31). The subsidiary cells of each stoma has a similar ultrastructural organization of the cuticle (Plate V, 32). The outer cycle has strongly developed papillae (Plate V, 30, 32) that overarch the orifice.

Papillae on normal epidermal cells of the lower cuticle have different shapes (Plate VI, 34, 35), but are always hollow. They are more developed and crowded in stomatal areas (Plate VI, 36). They consist of two well developed layers (*A*, *B*) with a diffuse interface between (Plate VI, 37). The outer layer has an external lamellated sublayer (*A*1). Lamellae are compact, parallel to the surface and separated by thin channels (Plate VI, 38). The innermost channels may arch up to 90° and extend into the homogeneus *A*2 sublayer (Plate VI, 38) in bands of 3–4 units. This sublayer demonstrates the same isodiametric transversely elongated translucent areas described earlier (Plate VI, 38). The lower layer (*B*) consists of an upper lamellated sublayer (*B*1) consisting of subparallel, straight to sinuous narrow units (Plate VI, 39, 40). An interface separates this sublayer from a basal granulose *B*2 sublayer (Plate VI, 40). This sublayer projects into the hollow interior of the papilla in the form of acute teeth (Plate VI, 37). This structure is probably related to the endostriae observed in transmitted light.

Comparisons

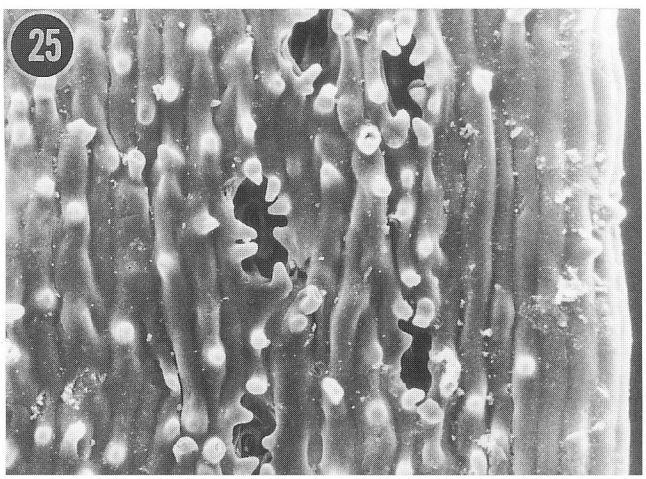
The specimens described here are included in the genus *Pseudoctenis* Seward emend. Harris (1964), rather than *Ctenis* Lindley and Hutton (1834) that has similar pinnae but with anastomosing venation. Another frond with the same general leaf morphology is *Pterophyllum* Brongniart, but it can be distinguished by a cuticle with syndetocheilic stomata. Two *Pseudoctenis* species are known from the same formation: *P. dentata* Archangelsky and Baldoni and *P. crassa* Archangelsky and Baldoni (Archangelsky and Baldoni, 1972). *Pseudoctenis dentata* differs in the toothed pinna apex and much smaller pinna size (up to 3 times smaller than *P. ornata*), as well as various cuticle characters including: epidermal cells on upper cuticle with sinuous anticlinal flanges, lack of papillae and hairs, stomatal distribution.

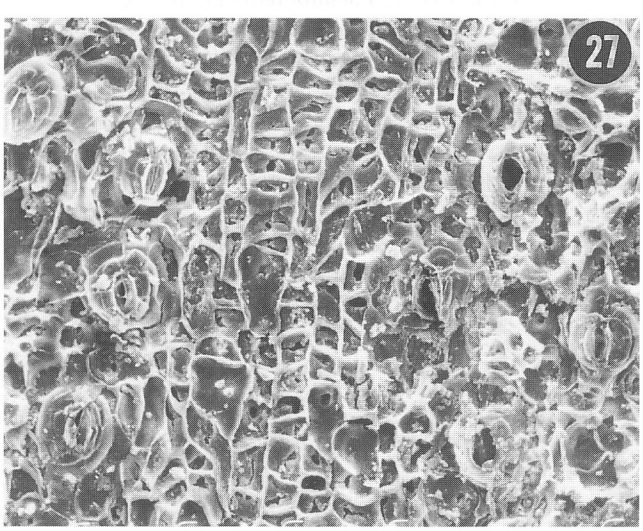
PLATE III

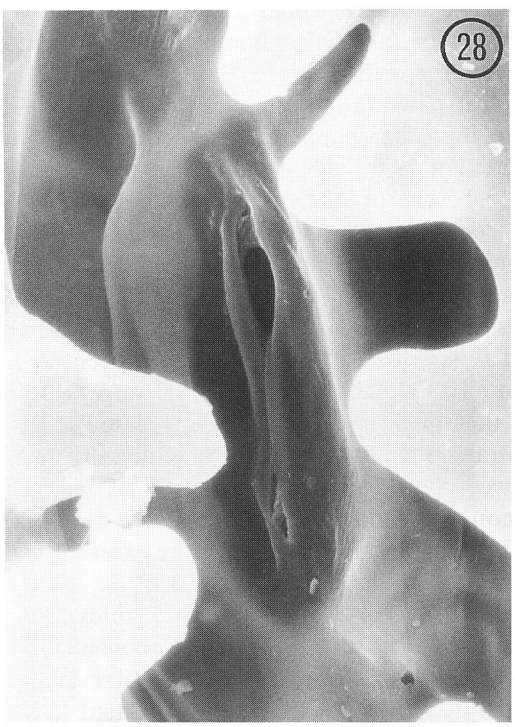
Lower cuticle (slides BA Pb p.m. 86, 88).

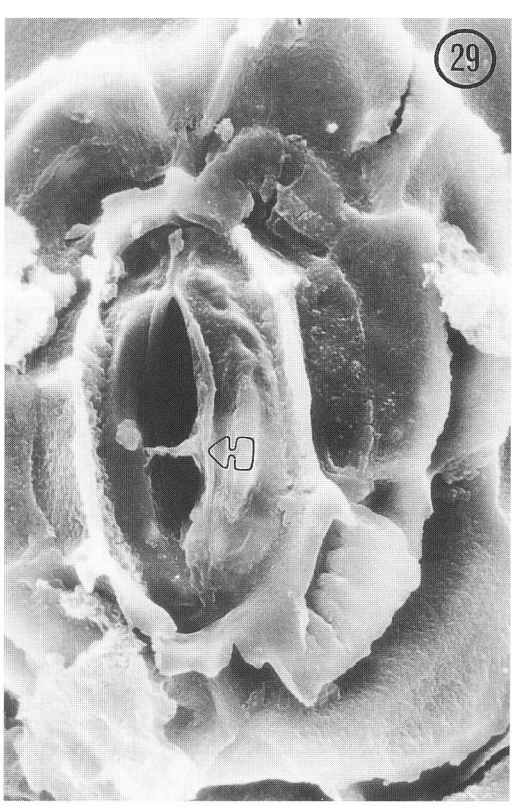
17. Epidermal cells forming vein and intervein longitudinal bands. × 100.
18. Neighbouring stomata sharing subsidiary cells. × 20.
19. Papillae protecting stomatal mouth. Note two lateral, more developed papillae and papillae endostriations. × 550.
20, 21. Epistomatal chamber of a stoma: two focal planes that show several subsidiary cells cycles. × 550.
22, 23. Guard cells of a stoma: two focal planes that show dorsal thickening at the pole (22) and in central area (23). × 550.
24. Lateral papilla at the stomatal mouth showing endostriae. × 550.

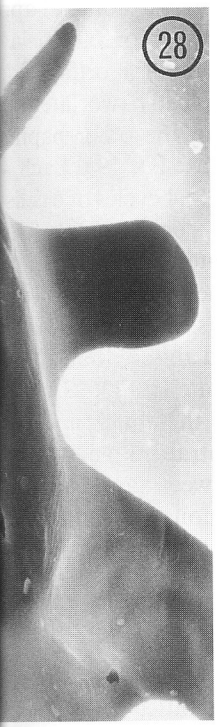
PLATE IV

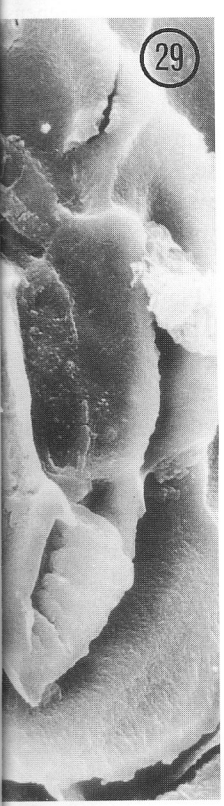












Pseudoctenis crassa, based on isolated leaf pinnae differs in having thicker veins (1.1 mm thick against 0.6 mm in *P. ornata*) and low vein density (1.1 per mm against 1.7 per mm in *P. ornata*). The thick cuticle in *P. crassa* (more than 20 μm), the lack of papillae on the upper cuticle, monocyclic or imperfectly dicyclic stomata, presence of pluricellular hairs, are additional characters that can be used to separate the species from *P. ornata*.

There are no other *Pseudoctenis* species known with preserved cuticles from Argentina. Halle (1913) described 2 species from the Jurassic Hope Bay Antarctic flora: *P. ensiformis* Halle and *P. cf. medlicottiana* (Oldham and Morris). Gee (1989) united both species as *P. ensiformis*. There is some resemblance to *P. ensiformis* including the slightly ensiform shape of pinnae, general width of the leaf, basal expansion of the pinna lamina, anadromic and catadromic sides and in the straight veins that reach the apex. However, there are significant differences: our species has a much thicker leaf rachis (7 mm against 2–3 mm), lower number of veins per pinna (8 against up to 12), thinner pinnae (0.8 cm wide against up to 1.6 cm) and no vein bifurcation. This would be the closest species in general leaf morphology to *Pseudoctenis ornata*.

Several Triassic species of *Pseudoctenis* are known as impressions in Argentina. Artabe (1986) presented a key using only general leaf morphology characters of 29 species, most found in Argentina. All show morphological differences with *P. ornata*. Among these, *P. ctenophylloides* Bonetti (Bonetti, 1968) from Barreal, San Juan Province, has 3–4 veins per mm and different shaped pinnae, and *P. grandifolia* from Los Menucos, Río Negro Province, has wider pinnae and a greater vein density per mm (2.6).

The type species of *Pseudoctenis*, *P. eathiensis* (Richard) Seward from the Late Jurassic of Scotland has been recently redescribed by van Konijnenburg-van Cittert and van der Burgh (1989). It differs in its larger size and more separate pinnae which are strongly decurrent on their catadromic side. Veins in *P. eathiensis* sometimes fork. The principal difference concerns the lower cuticle of the type species which lacks trichomes and/or papillae. *Pseudoctenis ornata* has a dense ornamentation that protects stomata and is also present on common epidermal cells.

There are several species of *Pseudoctenis* known with cuticle from the Yorkshire Jurassic flora (Harris, 1964). *Pseudoctenis locusta* Harris and *P. oleosa* Harris differ in the size and shape of pinnae, and each is characterized by a constricted base. *Pseudoctenis herriesi* Harris has larger pinnae with a truncate to obtuse apex and a higher vein concentration (25 or more veins per cm). *Pseudoctenis lanei* Thomas is most similar to *P. ornata* but differs in having slightly contracted pinna bases, wider petiole (10–15 mm) and thinner cuticle (2 μm) that almost lacks trichomes.

The cuticle of *Pseudoctenis florinii* Lundblad, from the Rhaeto-Liassic of Sweden, differs from the Patagonian species by the shape of the leaves, wider pinnae, more veins and the absence of papillae.

6. Discussion

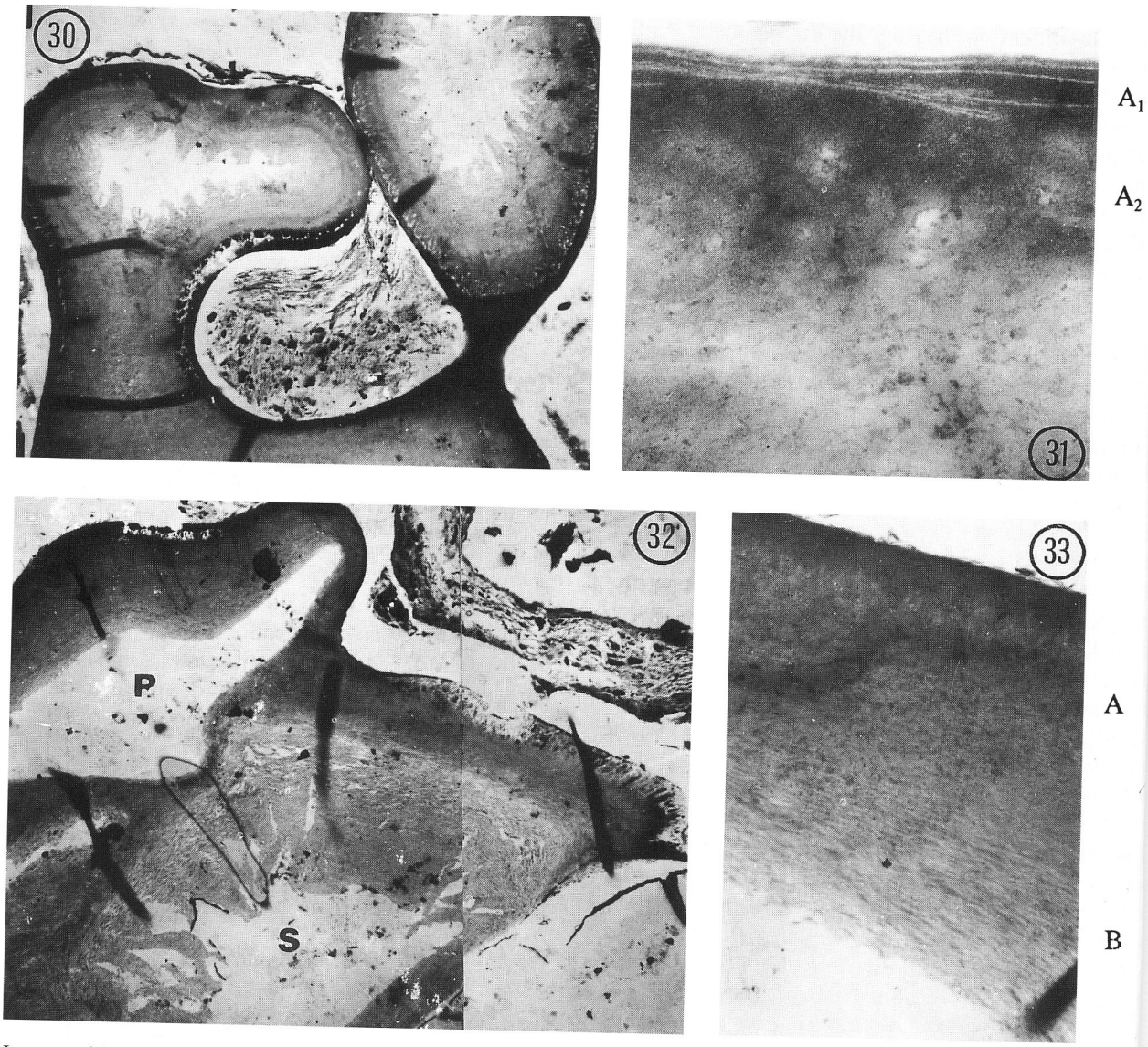
Historically it has been assumed that the cutinized fossils recovered from the Lower

PLATE IV

Lower cuticle.

25. External view to show stomata orientation, longitudinal ridges and distribution of papillae. The margin of the pinna is at the right of the picture. × 150.
26. External view showing a circular hole (trichome base) surrounded by papillae. × 1000.
27. Internal view to show stomatal bands (left and right sides of picture). × 150.
28. External view of a stoma showing papillae surrounding mouth of pit, dorsal thickening of guard cells and thickened mouth of the stoma. × 1500.
29. Internal view of a stoma. Note cycles of subsidiary cells and guard cells united by a ridge (arrow). × 1500.

PLATE V



Lower cuticle.

30. Section of two papillae overhanging mouth of epistomatal chamber. Note different layers that have contrasting staining and shape. ×2000.
31. Sections of cuticle. External part of cuticle showing outermost lamellae (*A1*) and a homogeneous internal area (*A2*). ×80,000.
32. Orifice of a stoma. Section of a portion of the mouth to show an overhanging papilla (*P*) and part of a subsidiary cell (*S*). Note the variation in staining of cuticle layers. ×2000.
33. Cuticular membrane. A section to show layers of the cuticle *A* and *B*. ×10,000.

Member of the Baqueró Formation were related to a fluvial paleoenvironment, influenced by a strong volcanic activity (Archangelsky, 1967; Archangelsky and Taylor, 1986). The present study adds new data, especially in regard to the physical environment in which these plants lived and subsequently died. The pyroclastic episode containing the plants is 2–3 m thick and composed by air-fall

tephra (tuffs) showing no signs of blast deposits at the base or within the body. The vent from which volcaniclastic material was expelled must have been located at some distance from the collecting site. Extrusion may have been caused by one or more volcanoes based on the ash load involved, especially if ash deposits formed during the eruptions of Mount Saint Helens (USA, 1980) or El Chichón (Mexico, 1982) (Spicer, 1989) are compared. Burnham and Spicer (1986) measured ash deposit sequences in El Chichón and concluded that although variation is present in thickness is typically not more than 1.0 m. This would also appear to be the case for similar deposits formed during a recent eruption of the Hudson volcano in Western Patagonia (1991; pers. observ.).

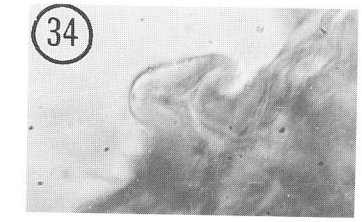
The base of our sequence is a paleosol developed over fluviatile sediments that belonged to a meandering river system, i.e. a more or less mature environment. The vegetation found in the Lower Member of the Baqueró Formation is variable and probably attained, or was close to attaining, its climax. Several plant groups were at their maximum diversification, and include conifers, bennettitales and some fern families. A few pteridosperms were still present. These sediments also represent the site of the first angiosperms from the Southern Hemisphere. To this scenario an increase in volcanic ash in fluviatile deposits was added. This participation persisted along the succession while vegetation almost waned during the final stages of the sequence, i.e. in the upper member of the formation.

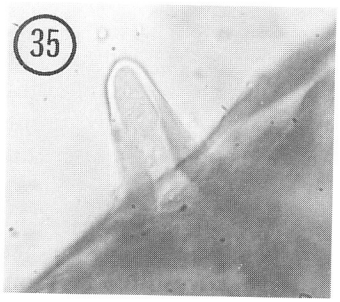
Pseudoctenis ornata lived in a fluvial valley (flood plain facies) under mild climatic seasonal conditions (as demonstrated by facies belonging to well developed channels, related flood plains and small shallow lakes). The associated kaolins suggest that the climate during this epoch was humid and hot-temperate (Cravero and Dominguez, 1993). Such associated plants as *Araucaria grandifolia*, *Taeniopteris* sp. and *Gleichenites* were also abundant and probably constituted the main ground cover. This association differs considerably from that found in other facies of the same formation. For instance, plant associations in lake/pond facies include other conifers (*Brachyphyllum*, *Trisacocladus*, *Nothopehuen*, *Squamastrobus*), ginkgoales, bennettitales, Osmundales, water ferns, Selaginellales, Isoetales, etc.

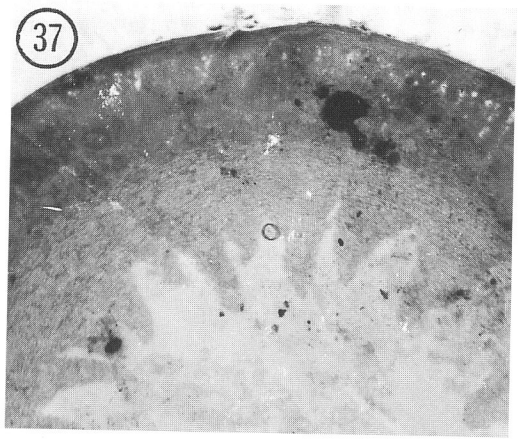
The *Pseudoctenis* association grew on a soil formed and developed by a continuous volcanic activity that produced increasingly thick ash deposits. The plants lived on the plain until they were buried in ash. When ash fall ceased, probably in a relatively short time a soil layer was newly formed that supported the same vegetation components. The depositional episode described here is found repeatedly in the studied section suggesting that volcanic activity was periodic. This general description coincides with observations of a recent eruption of the Hudson volcano (J. Genise and H. Corbella, pers. commun.) that happened at approximately the same location, and covered a vast region of Patagonia causing damage to animal and plant life. Thick ash layers from the Hudson eruption are still found covering vegetation in wind protected areas at a distance of over 100 km from the source. During a few days trees were covered with a heavy ash load and subsequently collapsed, falling in roughly the same direction as a result of wind. Bushes and grasses were also completely covered resulting in a complete crop loss. Two years later, however, as a result of human activity, crops were renewed. Although this process may be slower in natural conditions, plants may recover after one to two years in volcanic environments (Spicer, 1989). Ferns are the first colonizers in places a few hundred meters distant from the vent. This confirms that reproduction and dispersal by isospores is one of the best strategies for survival in drastic (catastrophic) conditions (Spicer et al., 1985). Although on a much smaller scale, the Hudson eruption represents a similar process to that responsible for the fossilization of *Pseudoctenis ornata*.

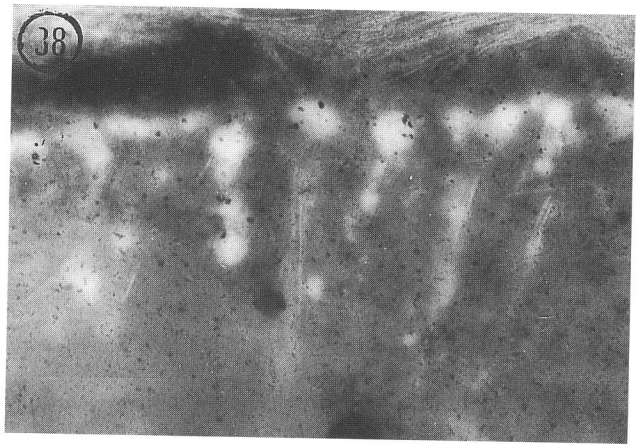
Preservation of *Pseudoctenis ornata* points to cool ash fall since there is no evidence of charring on the cuticle. A seasonal climate with periodical flooding of plains, combined with abundant atmospheric ash and soils rich in siliceous mineral, probably influenced plant growth and structure. Ash content in soils produced increased availability of nutrients providing short-term vegetation development. At the same time atmospheric ash overload was influencing the shape and structure of

PLATE VI



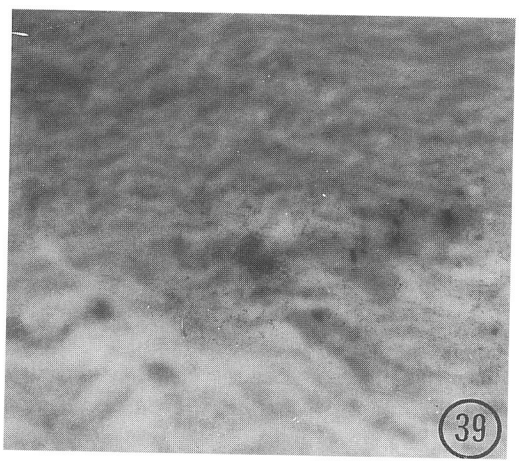


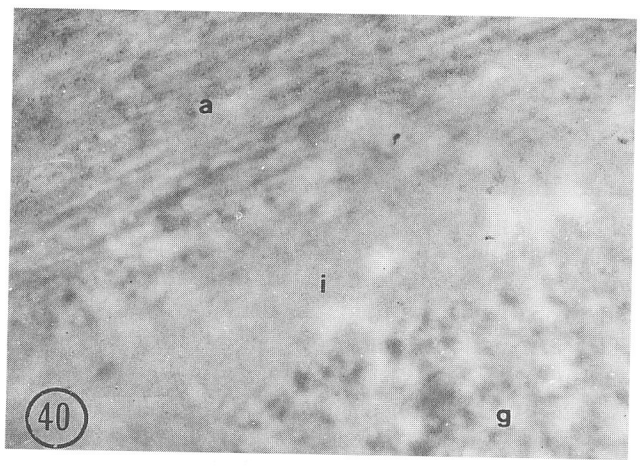




A1

A2





the cuticle and epidermis. This environmental stress may be related to leaf and cuticle xeromorphic features.

Cook et al. (1981) have shown that ash fall and subsequent accummulation may result in a number of effects in plants. Some of these include: **stress** due to weight of the ash, **reduction** in overall photosynthesis due to stomatal clogging and the presence of ash as a barrier to light, **cooling** due to surface reflectance from the ash and short-term increase in negative water potential because of mechanical damage. Stomatal clogging, sunken guard cells, orifice and dorsal thickenings on guard cells, cuticle thickness (periclinal walls and anticlinal flanges), connecting ridges between guard cells, channeled external surface on upper cuticle and margins of lower cuticle, together with abundant, small hollow papillae, represent xeromorphic characters. Some of these characters have been found in cycadalean plants from this formation. *Mesodescolea plicata* (Artabe and Archangelsky, 1992), *Pseudoctenis dentata*, and *P. crassa* (Archangelsky and Baldoni, 1972) have conspicuous dorsal thickenings on exposed guard cells. Sunken guard cells are characteristic of *Ticoa harrisii* (Archangelsky et al., 1986). Plants belonging to other gymnosperm groups represented in this formation also show strong xeromorphic characters, such as the deep stomatal chambers in *Tarphyderma glabra* Archangelsky and Taylor (Archangelsky and Taylor, 1986) and *Mesosingeria* spp. (Archangelsky, 1963).

The cuticle characters of *Pseudoctenis ornata*, when considered in a paleoenvironmental context, probably reflect temporary adverse growing conditions. As a result they may be interpreted as in a "state of adaptation", not functioning in optimal conditions (Knoll and Niklas, 1987). Such xeromorphic characters as reflected by the cuticle in *Pseudoctenis ornata* may have been useful adaptations that allowed the plants to cope with stress produced by ash fall on leaves.

Heavy ash fall also influenced the structure and short-term development of soils. An eventual return to previous atmospheric and edaphic conditions was a problem for the plants because their readaptation may have involved a change of those xeromorphic characters.

7. Conclusions

Evidence is slowly accumulating that suggests that during the Early Cretaceous plant life was strongly influenced by volcanic activity in a vast area of Patagonia. The source area of the persistently falling ash was located to the west where volcanoes occur today. Different paleoenvironments (e.g. lacustrine, fluvial, flood-plains) variously impacted plant communities by changing edaphic patterns and atmospheric conditions. The cuticle of several gymnosperms, including *Pseudoctenis ornata*, have features that strongly suggest the plants were living under conditions of stress. All evidence points to ash as the primary cause for this stress. This effect persisted during the deposition of the Baqueró Formation. At the early stages (lower member) plants easily survived by developing protective structures while soils had enough nutrients to support them. The gradual increase in ash fall is evidenced in the tuffaceous composition of the upper section of the unit (upper member). It shows that soil development and the formation of plant bearing horizons became increasingly rare, and eventually disappeared. *Pseudoctenis ornata* is found in conditions that suggest transition in disposition within the stratigraphic column.

PLATE VI

34, 35. Two papillae of a different shape (slide BA Pb p.m. 86). × 550.
36. External view of lower cuticle to show high density of papillae around stomata. × 500.
37. Section of a papilla showing layers of cuticle. × 8000.
38. A detail showing outer lamellae and *A*2 sublayer. Note arching of lamellae in middle of picture. × 50,000.
39. *B*1 sublayer showing sinuous units. × 50,000.
40. *B*1 sublayer (*a*), interface (*i*) and granulose *B*2 sublayer (*g*). × 50,000.

Finally, *Pseudoctenis ornata* represents an addition to the list of cycadalean species described from this formation. Studies now in progress are directed at leaf variation among taxa of this order that demonstrate that the Cycadales occupied several ecological niches and were important components of plant communities during the Early Cretaceous in Patagonia.

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